A PHYLOGENETIC STUDY OF THE LARVAL AND ADULT HEAD IN NEUROPTERA, MECOPTERA, DIPTERA, AND TRICHOPTERA.*

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Since practically all of the recent attempts to trace the phylogeny of insects have been based upon the study of the wing veins, which are extremely variable features within the same order, or even family, of insects, it has seemed advisable to examine other less variable structures, and those from widely different parts of the body, in order to ascertain if such a study would confirm or disprove the conclusions reached from a study of the wing veins alone. The present paper is therefore offered as one of a series in which the various structures which appear to be the most useful for a phylogenetic study, have been compared in the Neuroptera, Mecoptera, Diptera and Trichoptera. Many of the accompanying rough sketches were made from material kindly loaned to me by Dr. N. K. Banks, to whom I am deeply indebted for many valuable suggestions, and for the privilege of examining the specimens in his unusually extensive collection of Neuroptera, Mecoptera, and Trichoptera. I am also greatly indebted to Dr. C. W. Johnson for the identification of the Diptera used in the preparation of this paper.

It is customary to speak of this or that single type as the ancestral one for a large group of insects, but I think that this is a mistaken conception, since a study of the ancestral groups (or rather, those which have departed but little from the condition characteristic of the ancestors of other insects) would indicate that the ancestral forms frequently differed quite markedly among themselves, exhibiting *several* developmental tendencies (instead of merely one type) which frequently manifest themselves in the evolutionary series of the forms derived from them. As an illustration of this view, I would call attention to the "short-headed" series of Neuroptera, Mecoptera, and Diptera shown in Figures 1, 2 and 3, and the "long-headed" series of the same groups of insects shown in Figures 4, 5 and 6. These

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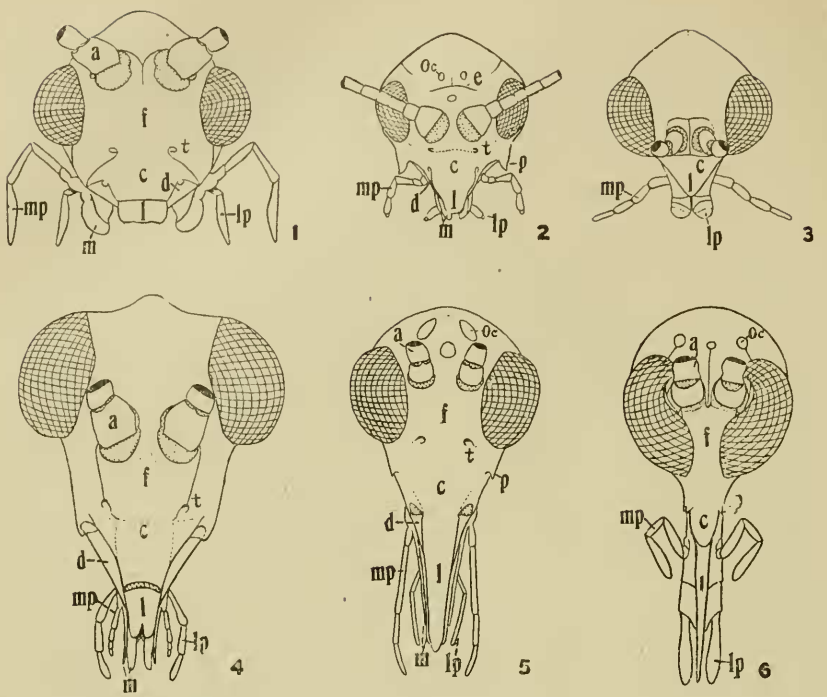

Fig. 1. Head of the Neuropteron *Hemerobius.*
Fig. 2. Head of the Mecopteron *Panorpodes.*
Fig. 3. Head of the Dipteron *Erioptera armata,* O. S.
Fig. 4. Head of the Neuropteron *Nemoptera.*
Fig. 5. Head of the Mecopteron *Bittacus.*
Fig. 6. Head of the Dipteron *Asyndulum montanum* Roeder.

In all cases, excepting figures 12 and 13, the head is drawn in frontal view. In some figures only basal segments of antennæ are drawn. The areas of cross-hatching denote the compound eyes.

ABBREVIATIONS.

a—Antenna, or basal segments of antenna.
ac—Anteclypeus.
c—Clypeus, or clypeal region.
d—Mandible.
e—Epicranial suture.
f—Frontal region.
l—Labrum, or labral region.
lp—Labial palpus, or terminal portion of labium.
m—Maxilla.
mp—Maxillary palpus.
o—Occipital region.
oc—Ocelli.
p—Genal process.
t—Tentorial or frontal pits.
x—Plical process, or point of attachment of cervical fold.
y—Line of attachment of cervical fold or plica.

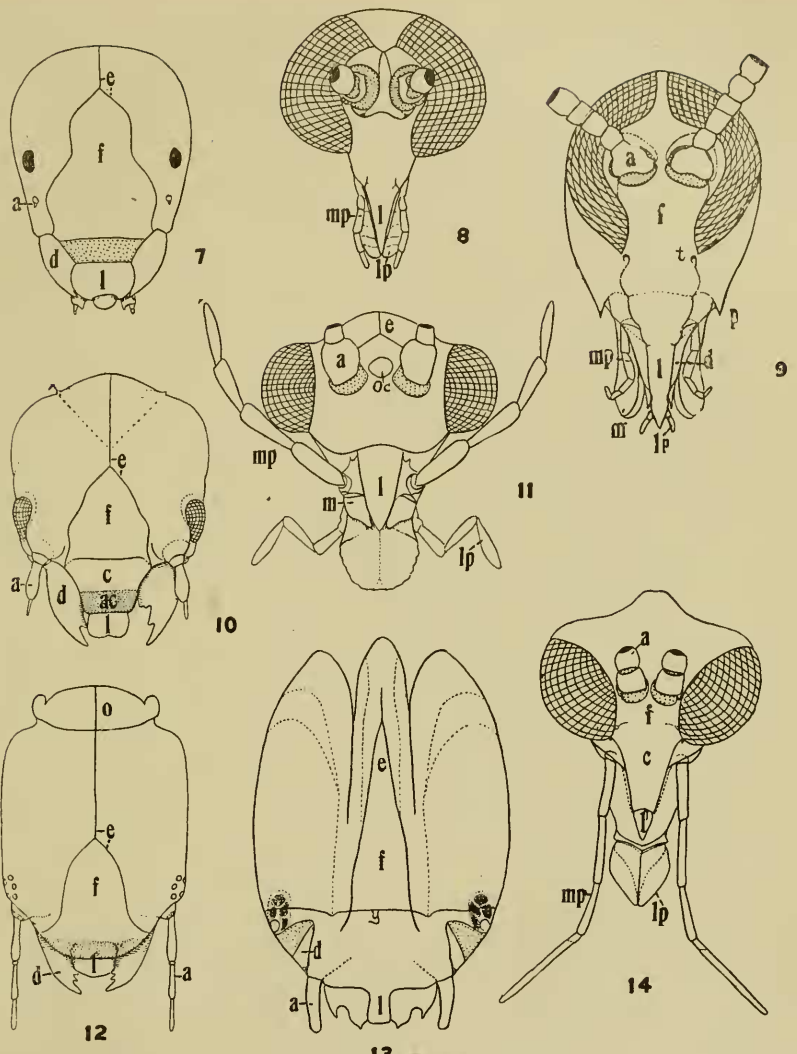

Fig. 7. Head of a larval Trichopteron.
Fig. 8. Head of the Dipteron *Heteromyia* (Ceratopogon) *trivialis*, Loew.
Fig. 9. Head of the Mecopteron *Merope tuber* (male).
Fig. 10. Head of a larval *Panorpa* (Mecopteron).
Fig. 11. Head of the Trichopteron *Neuronia*.
Fig. 12. Head of a larval *Raphidia* (Neuropteron).
Fig. 13. Head of a larval Tipulid.
Fig. 14. Head of the Dipteron *Bittacomorpha* (based upon the species *clavipes* and another *Bittacomorpha*).

series show very clearly that in the Neuroptera (among which are found certain forms which have departed but little from the ancestral condition of the Mecoptera) instead of merely one type, there are at least two developmental tendencies, the one leading to a retention of a shorter type of head such as that of the Neuropteron shown in Fig. 1, while the other leads to the formation of a more elongate type of head, such as that of the Neuropteron shown in Fig. 4. These two tendencies are carried over, or re-appear, in the Mecoptera, which are descended from Neuropteron-like forebears. Thus the short-headed type is retained in such Mecoptera as that shown in Fig. 2 (which, however, exhibits a slight tendency toward a narrowing and lengthening of the lower portion of the head), while the tendency toward the formation of the elongate type of head appears again in such Mecoptera as that shown in Fig. 5. Similarly, in the Diptera, which in turn are derived from Mecopteron-like forebears, the same two tendencies reassert themselves, some of the Diptera having retained the short-headed type, as shown in Fig. 3, while other Diptera, such as the one shown in Fig. 6, have developed the elongate type of head.

It might be argued that a similar mode of life, or similar "environmental" conditions might cause a marked similarity in outline in the heads of the insects in question, and that this similarity is therefore due to a convergence—or rather to a parallelism of development. However, the marked morphological similarity in a series of structures taken from widely separated parts of the body (e. g. mouthparts, thoracic sclerites, legs, terminal abdominal structures, etc.) and the marked resemblance which extends even to the more minute details, and in parts which are not much used, or are not of vital importance to the organism, would preclude the possibility of a mere parallelism of development—which might possibly be the case if we were dealing with a single set of structures alone; but to argue that a parallelism of development has brought about the similarity in structure between all of these parts of the body in the series, is demanding too much of chance and the "law of probability."

While claiming that the series of insects represented in Figs. 1, 2 and 3 and the series represented in Figs. 4, 5 and 6, to all intents and purposes serve to illustrate what has actually

happened in the evolution of the head region of certain Diptera, I would not imply that recent Diptera are descended from recent Mecoptera, or that living Mecoptera are descended from living Neuroptera. On the other hand, it is quite true that living Neuroptera, Mecoptera, and Diptera have travelled together along the same developmental "road," so to speak, in following out certain evolutionary tendencies. At some point along the road, the Neuroptera branched off to follow their own path of specialization, but some of them wandered but a short distance from the main line, and have remained as little changed as certain of the fossil forms which fell by the wayside at an early date. These "conservative" individuals have preserved many features characteristic of the ancestors of the Mecoptera and Diptera who continued together for a greater distance along the road of evolution, before the Mecoptera in turn branched off to follow their own path of specialization. So too, among the Mecoptera certain individuals wandered but a short distance from the main line, and have preserved many features characteristic of the ancestors of the Diptera, and the same process was repeated when the Dipteron-like ancestors of the fleas gave rise to the Siphonaptera. The study of these "conservative" forms among living insects is quite as instructive as the study of fossil forms, and has the additional advantage of enabling one to examine the minute details not preserved in the fragmentary fossil remains, and to take into account the biological habits, etc., which are of considerable importance in an attempt to determine the relationships of the different groups of insects.

In the head region of nearly all adult Mecoptera, there is a well marked tendency toward the formation of a "genal process" or protuberance of the lower portion of the genæ ("p" of Figs. 2, 5 and 9), and it is rather strange that such a widespread tendency in the Mecoptera should not reappear in the Diptera—although the process of the genal region labeled "p" in the Dipteron shown in Fig. 6 may be homologous with the genal process of the Mecoptera. In some of the Mecoptera (Fig. 9) there is a tendency for the eyes to extend upward toward the top of the head, and downward toward the mesal line below the antennæ, and the same tendency is evident in the Diptera shown in Figs 8 and 6.

In some Diptera (Fig. 14) the contour of the upper portion of the head is more like that of certain Neuroptera (Fig. 4), while in other Diptera (Figs. 6 and 8) it is more like that of certain Mecoptera (Figs. 5 and 9). On the whole, the basal segments of the antennæ of the Diptera (Figs. 6 and 14, "a") are more like those of the Mecoptera (Fig. 5), and the resemblance between the antennal segments of the Mecopteron *Merope* and those of certain Mycetophilids and other Diptera is very striking, as I am hoping to show in a subsequent paper. In these respects, the Trichopteron shown in Fig. 11 is more like the Neuroptera than it is like the Diptera and in general the statement would hold true, that the Mecoptera approach the Dipteron type far more closely than the Trichoptera do, and are therefore in all probability much more closely related to the Diptera than the Trichoptera are, although the Trichoptera also have carried over certain "ancestral" features from the common ancestral group which gave rise both to them and to the Mecoptera and Diptera, so that they cannot be entirely disregarded in a phylogenetic study of the insects in question.

Although the labial palpi "*lp*" are much larger than the maxillary palpi "*mp*" in the "long-headed" Neuropteron shown in Fig. 4, the maxillary palpi "*mp*" are much longer than the labial palpi "*lp*" in the Neuropteron shown in Fig. 1, and in most Mecoptera (Figs. 2, 5 and 9) and Diptera (Figs. 3 and 14) this is likewise the case, as is also true, to a lesser degree, in the Trichopteron shown in Fig. 11. There is thus apparent in the Mecopteron and Dipteron stocks a marked tendency toward the reduction of the labial palpi, and the glossæ and paraglossæ tend to disappear, although I am not certain that neither paraglossæ nor glossæ are well developed in the Diptera, since Peterson, 1916, who has examined a wide range of Diptera, thinks that glossæ and well developed paraglossæ are to be found in this group. On the other hand, if one examines a specimen of *Bittacus* and *Panorpa*, it is quite evident that the maxillæ (excepting the palpi) are reduced, or have begun to unite with the labium, and that the glossæ and paraglossæ of the labium have almost disappeared, while the labial palpi have become approximated in the median line, thus assuming a condition suspiciously like that exhibited by the Dipteron shown in Fig. 6. A study of the embryological development

of the parts in question is necessary before this point can be definitely determined but the "phylogenetic" evidence would indicate that Peterson's interpretation of some of these structures may need revision. A detailed comparison of the mouthparts, accompanied by drawings of the insects in question, will be published later, as a part of the series dealing with the phylogeny of the Diptera, Mecoptera, etc., so that it is unnecessary here to do more than call attention to the tendency toward an elongation of the mouthparts exhibited by certain Neuroptera (Fig. 4), and developed to a greater extent in certain Mecoptera (Fig. 5), while it is carried to an extreme in the Culicids and other Diptera.

A comparison of the heads of the larvæ under consideration has thus far been rather disappointing, due to the fact that it is necessary to examine a far wider range of forms than is at present available, in order to select those which have preserved the desired characters—and it is largely a matter of chance whether one is so fortunate as to find these or not. I have no Culicid or Chrysopid larvæ at present, but I recall having observed in them a "cervical plica," or fold of the membranous region of the neck, which projects over the head capsule for a short distance and is attached to it at the point labeled "x" in Fig. 10 of a Panorpid larva. In some of the Trichopterous larvæ which I have examined, a similar "cervical plica" is attached to either side of the head capsule, but it is not so well developed in the Trichoptera. It is possible that a further overgrowth of the head capsule by the neck-fold mentioned above, has resulted in the condition exhibited by the Tipulid larva shown in Fig. 13, in which a fold of the neck membrane has grown over the head capsule, to which it is very closely applied, as far forward as the line labeled "y" in Fig. 13.

As far as the head region of the larvæ is concerned, the Diptera seem to be about as similar to the Neuroptera as they are to the Panorpids, and the head of a larval Panorpid is somewhat more "Neuropteron-like" than the head of a larval Trichopteron is. In the case of the adult head, however, the Diptera are closer to the Mecoptera than to the Neuroptera, and also appear to be very much closer to the Mecoptera than to the Trichoptera. In conjunction with the study of such other features as the antennæ, mouthparts, thoracic sclerites, legs,

terminal abdominal structures, etc., a comparative study of the head capsule in the insects in question would indicate that the line of development of the Trichoptera branched off from the common ancestral "Neuropteroid" stem at a point not far distant from the origin of the Mecopteron line of development. The ultimate ancestors of the Diptera were Neuropteron-like (the tendency toward the reduction of the hind wings occurring regularly in such Neuroptera as *Nemoptera*, and occasionally in such forms as *Psectra, etc.*) and they were related to both the ancestral Trichoptera and Mecoptera. The Dipteron line of development, however, has paralleled that of the Mecoptera remarkably closely (more so in fact than any other insects) and since the Mecoptera have "lagged behind," or have not travelled as far along the road to specialization as the Diptera have, they have remained in many respects strikingly like the ancestors of the Diptera, so that a study of their structures will frequently serve to indicate the steps by means of which the more highly modified homologous structures in the Diptera have reached their present state, in following out certain evolutionary tendencies present in both lines of development.

BIBLIOGRAPHY.

1895. **Felt**—The Scorpion Flies: Report State Entomologist, N. Y., 10, 1895, p.463.

1913. **Miyake**—Studies on the Mecoptera of Japan: Jour. Coll. Agr. Imp. Univ. Tokyo, 6, No. 6, p. 265.

1916. **Peterson**—The Head Capsule and Mouthparts of Diptera: Ill. Biol. Monographs, Vol. 3, No. 2, p. 1.

A more complete list of the articles dealing with the mouthparts and phylogeny of the insects under consideration will be given in articles dealing with these phases of the subject.